

ishment for opportunistic species (Emerson & Grant, 1991). Hydrodynamic factors are also known to be important in the dispersal of larval bivalves and can result in patchy recruitment events. Bedload transport of juvenile soft-shell clams *Mya arenaria* Linnaeus, 1758, can affect population dynamics by immigration of large aggregations into underutilized habitats (Emerson & Grant, 1991). The common cockle *Cerastoderma edule* Linnaeus, 1758, lives in the top few centimeters of sediment, and the combined stressful effects of waves, currents, and burial have been shown to cause the emergence of large numbers of these clams, thereby enhancing the likelihood of their passive entrainment and transport (Richardson et al., 1993). Scallops are notorious for their locomotory ability whereby adults can swim horizontally and migrate to new habitats (Carsen et al., 1995). Juveniles, however, swim vertically and are then advected horizontally by currents and possibly moved into more hospitable habitats (Carsen et al., 1995). The accumulation of *Mulinia lateralis* described here was composed of adult individuals, providing evidence of the importance of adult dispersal in bivalve population dynamics.

### IMPLICATIONS

Observation and reporting of unexpected ecological phenomena such as the one described here can provide valuable information about population ecology and life history of organisms, as well as information useful for interpretation of fossil assemblages (Boyajian & Thayer, 1995). Although population studies and transplantation experiments provide useful information about a species, unrecorded episodic events can produce effects that could subsequently appear in a population and lead to erroneous conclusions regarding range and cohort dynamics. For example, the size-selective mass exhumation of a portion of a bivalve population could leave a population with the length frequency skewed toward older (or younger) individuals. Future age-class analyses could record this as a low recruitment event, when, in fact, recruitment was normal for the size classes affected by the exhumation.

Interpretation of fossil assemblages could be biased by deposition of large numbers of live animals as well as dead shells (Levinton, 1970; Rollins et al., 1992; Aguirre & Farinati, 1999; Walker & Goldstein, 1999). Although we do not have any information on the post-depositional fate of this assemblage, we do know that the sandy intertidal beach is not ideal habitat for *Mulinia lateralis* (Levinton, 1970). Morris & Rollins (1977) described some life-positioned bivalve fossil assemblages on St. Catherines Island. Interpretation of such fossil assemblages must take into account the history of the assemblage prior to death as well as that after death (taphonomy). The majority of these *M. lateralis* were alive, but their condition could have been weakened by the stresses from exhumation, transport, deposition, and desiccation

in the intertidal zone in such high densities. If this assemblage remained intact and was buried on the beach, it could be misinterpreted as an in situ population. Alternatively, the assemblage could be interpreted as a transported death assemblage. Some of the live clams were in life position and could be misinterpreted as having recruited to this habitat as juveniles rather than adults (Rollins & West, 1997; West et al., 1990). There are many ways that this event could be interpreted that could lead to rational but erroneous conclusions. Documentation of these events can provide useful information about a species, community or fossil assemblage, and have bearing on shellfisheries' predictions, yields, and harvests.

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## The Natural Diet of the Argentinean Endemic Snail *Chilina parchappii* (Basommatophora: Chiliniidae) and Two Other Coexisting Pulmonate Gastropods

A. L. ESTEBENET\*, N. J. CAZZANIGA AND N. V. PIZANI

Universidad Nacional del Sur, Departamento de Biología, Bioquímica y Farmacia, 8000 Bahía Blanca, Argentina

**Abstract.** In this paper we study the natural diet of *Chilina parchappii* (d'Orbigny) (Chiliniidae), *Biomphalaria peregrina* (d'Orbigny) (Planorbidae), and *Physa venustula* Gould (Physidae) in an artificial canal in the Province of Buenos Aires, Argentina. The close similarity between the organic particle composition of the sediment and the crop contents of the three species studied suggests they are basically non-selective feeders. The food composition does not differ from the *Anfwuchs* composition. Diatoms and detritus particles are the main food items for the three species. Although there is a high degree of diet overlap among the three species, a principal component analysis revealed interspecific differences in diet. *Biomphalaria peregrina* is more detritivorous; *Chilina parchappii* ingests more diatoms; and *Physa venustula* consumes more non-filamentous algae. Experimental analysis of the ingestion, egestion, and assimilation rates, and the assimilation efficiency suggests that the endemic *Chilina parchappii* is subject to a probable risk of competition in a case of food shortage. However, competition among snails is highly improbable in the present area of sympatry, i.e., the lower basin of the Napostá Grande stream, which is rich in detritus.

### INTRODUCTION

Periphyton and detritus particles are almost universal food items for freshwater gastropods. Although some selection against or for specific items can be found, pulmonates are predominantly non-selective feeders (Hunter, 1980; Madsen, 1992; Brendelberger, 1995, 1997).

Selective grazing by freshwater gastropods has, however, been proposed as a cause of shifts in the succession of the benthic algae (Tuchman & Stevenson, 1991) or changes in periphyton composition (McCollum et al., 1998). Whereas detritus was by far the most common item in the gut of 20 snail species in England (Reavell, 1980), *Planorbis vortex* (Linnaeus) specifically selected against detritus and for diatoms (Lodge, 1986). *Ancylus fluviatilis* (Müller) also preferred diatoms and other periphytic algae, and did not eat detritus or fungal hyphae (Calow, 1973a, b). Trophic strategies are therefore variable among the freshwater snails, according to environmental and functional conditions.

The most abundant species of pulmonate snail in the lower basin of the Napostá Grande stream (Buenos Aires Province, Argentina) are the recently introduced *Physa venustula* Gould, 1847 (Physidae), the native *Chilina parchappii* (d'Orbigny, 1835) (Chiliniidae), and *Biomphalaria peregrina* (d'Orbigny, 1835) (Planorbidae).

The natural diets of these three South American species have not been studied previously. Some extrapolations are possible from the literature showing that the Planorbidae

and Physidae show great ecological uniformity (Calow, 1973b; Hunter, 1980; Reavell, 1980; Kesler et al., 1986; Underwood & Thomas, 1990; Madsen, 1992; Carman & Guckert, 1994), but nothing is known at present about the feeding habits of the South American endemic family Chiliniidae. Species of Chiliniidae have been deemed to feed only on diatoms (Brace, 1983; Bosnia et al., 1990).

In this paper we study the natural diet of *Chilina parchappii*, *Biomphalaria peregrina*, and *Physa venustula* with the aim of determining whether they feed non-selectively and whether the diet of the invading species (*P. venustula*) overlaps those of the native species (*B. peregrina* and *C. parchappii*).

### MATERIALS AND METHODS

The sampling site is an artificial canal within Parque de Mayo, an urban park in Bahía Blanca city (38°44'S–62°00'W, Argentina). It is fed with water from the Napostá Grande stream. The selected portion of the canal is 70 m long and about 4 m wide, with a maximum depth of 0.60 m. The sediment is mostly sandy silt, with a high proportion of detritus. The macrophytes *Myriophyllum elatinooides* (L.), *Potamogeton striatus* Ruiz & Pavon, and *Chara contraria* A. Braun ex Kütz. form dense mats in the center of the canal during most of the year. The biomass of the former two species decreases dramatically in winter.

Sampling was performed on six dates from December 1992 to November 1993. Individuals of the three snail species were picked up by hand along the canal margins,

\* e-mail: estebene@criba.edu.ar

and immediately killed by immersion in hot water. The soft parts of the snails were extracted in the laboratory and frozen at  $-20^{\circ}\text{C}$  for further analysis. Freezing was the best procedure to preserve the ingested algae, as revealed by preliminary trials of different preservation techniques (alcohol, formaldehyde, FAA, freezing); the alterations produced by chemicals made it difficult to recognize food items.

In winter (July), only individuals of *Chilina parchappii* were found in the canal, and their digestive tracts were empty, except for a small quantity of mineral particles retained in the stomachs. This sampling season was therefore excluded from the comparative analysis.

To detect possible ontogenetic differences in the diet we defined two disjunct size classes for each species, as follows: *Biomphalaria peregrina* (maximum diameter), young  $< 7$  mm, adult  $> 13$  mm; *Chilina parchappii* (shell length), young  $< 7$  mm, adult  $> 17$  mm; *Physa venustula* (shell length), young  $< 5$  mm, adult  $> 8.7$  mm.

The natural diets were analyzed by spreading the contents of the rear portion of the esophagus or crop in a drop of distilled water, prior to their observation under a compound microscope at a magnification of  $\times 400$ . We examined four to 14 snails for each species and date. The algae were identified to the generic or specific level, but were grouped into six groups for quantitative analyses: blue-green algae (BG), diatoms (Di), filamentous green algae (F), non-filamentous algae (unicellular, paucicellular, or colonial) (NF), detritus (De), and sand (S). The presence of these six items was recorded on 20 randomly selected microscope fields per individual.

The volume of the crop contents varied among and within the snail species as a consequence of body size and the degree of gut fullness. Therefore, for each individual snail, we determined the proportion of microscope fields where each kind of food was recorded in relation to the sum of all the fields with positive records:

$$p_i = n_i / \sum n_i$$

where  $p_i$  is the relative proportion of fields with food  $i$ , and  $n_i$  is the number of fields containing the food  $i$  (Kesler et al., 1986).

On the first sampling date we took simultaneous samples of sediment and periphyton to investigate possible selective feeding by comparing them with crop contents. The samples were taken from three different sites by scraping or sucking with a pipette the surface where the snails were adhering to the substrate.

The crop contents of 154 dissected snails were analyzed by principal components (PCA), using the covariance matrix as input (Orlóci & Kenkel, 1985), to determine possible seasonal and specific variations in the snail diets.

Laboratory experiments were performed to quantify the ingestion rate, egestion rate, and assimilation efficiency of the three snail species. Only adult snails were used

in these trials. Forty-eight previously weighed glass slides ( $75 \times 25 \times 1.2$  mm) were placed in a periphyton sampling box, and immersed in an artificial shallow pond. Three weeks later, when a substantial growth of *Aufwuchs* was evident, the slides were transferred to the laboratory and washed with demineralized tap water to remove loose material. Algae attached to the slides were mainly diatoms (mostly *Navicula* spp.) and the disk-shaped green *Coleochaete* sp. For every gastropod species, nine groups of three snails each (previously starved for 24 hr) were placed in Petri dishes 95 mm in diameter, filled with 50 ml of demineralized tap water. Six groups received two colonized slides as food; the remaining three groups were used as controls (without food). Twelve colonized slides were immersed in similar Petri dishes, without snails, as a reference of non-predated periphyton biomass.

Snails were allowed to feed for 4 hours before slides were removed, washed, dried at  $60^{\circ}\text{C}$  for 48 hr, and weighed to the nearest 0.1 mg. During the feeding tests, the feces produced by the snails (feeders and control) were collected with a Pasteur pipette. After removal of the slides, fecal collection was continued for an additional 4 hours. The snails were then killed by immersion in hot water and their soft parts were extracted from the shells. Feces and soft parts were dried at  $60^{\circ}\text{C}$  for 48 hr, and weighed to the nearest 0.1 mg.

To quantify ingestion, egestion, and assimilation rates we used the following formulae:

$$\text{Ingestion rate} \quad \text{IR} = \text{TI}/\text{DW}$$

$$\text{Egestion rate} \quad \text{ER} = \text{TF}/\text{DW}$$

$$\text{Assimilation rate} \quad \text{AR} = \text{IR} - \text{ER}$$

$$\text{Assimilation efficiency} \quad \text{AE} = (\text{TI} - \text{TF}) \cdot 100/\text{TI}$$

Total ingestion (TI) represents the total amount of food ingested (in mg), and is calculated as the difference between the dry periphyton weight on the non-predated and predated slides after the feeding period. Total feces (TF) represents fecal production (in mg); it was corrected by subtracting feces produced by control snails. DW is snail dry weight (in mg). Mean values of IR, ER, AR, and AE of the three species were compared by one-way ANOVA on the transformed data (log transformation for the rates; arcsine square root for the efficiency). The *a posteriori* multiple comparisons were made by Scheffé tests.

## RESULTS

Although the basic morphology of the digestive system is the same in the three species, there are some differences in the strength and degree of differentiation of the stomach region. *Chilina parchappii* shows a striking contrast between the relatively broad, almost black crop opening to a strongly muscular, bulbous, pearl pink gizzard. The crop is also well differentiated in *Biomphalaria peregrina*, but the gizzard is less muscular. The stomach

of *Physa* is morphologically simpler, uniformly grey colored, with no clear differentiation between crop and gizzard, the latter being thin-walled.

Figure 1 shows the temporal variation of the whole crop contents of the three species. No ontogenetic differences were detected for any snail species with respect to trophic preference (test  $t$ ,  $P > 0.05$  in all cases). Because of this, data from young and adult snails were grouped for the rest of the analysis.

All snail crops contained some mineral particles (sand) that probably aid in grinding the food (mainly the diatom frustules). The proportion of mineral particles was, however, significantly different among the snail species ( $F = 16.82$ ;  $df = 2, 152$ ;  $P < 0.0001$ ). An *a posteriori* Scheffe's test showed that *Biomphalaria peregrina* was the species with the highest proportion of ingested sand, whereas no significant difference in sand content was detected between *Physa venustula* and *Chilina parchappii*.

The main food particles were detritus and diatoms in the three species. The most frequent diatoms were in the genera *Achnanthes*, *Cocconeis*, *Epithemia*, *Fragilaria*, *Gomphonema*, *Gyrosigma*, *Navicula*, *Nitzschia*, *Rhoicosphenia*, *Surirella*, and *Synedra*; with a lesser frequency we recorded the diatoms *Asterionella*, *Amphora*, *Cymbella*, *Diatoma*, and *Pinnularia*. The filamentous green algae were represented by *Cladophora* spp. and *Oedogonium* spp. The non-filamentous algae were *Scenedesmus* (constant in all dissected esophagi), *Ancystrodesmus*, *Coelastrum*, *Crucigenia*, *Oocystis*, *Pediastrum*, *Tetraedron*, and *Euglena*. The blue-green algae were always represented by *Chroococcus* and *Merismopedia*, but the filamentous *Anabaena* and *Oscillatoria* were also present in a lesser proportion.

We found fragments of macrophyte leaves (specifically *Potamogeton striatus*) in only two (1.3%) of the 154 analyzed crops.

While radular teeth were seldom found in the crop contents of *Biomphalaria* and *Physa* (4.9% and 5.7% of the crops, respectively), 46% of the stomachs of *Chilina parchappii* contained radular teeth, mainly marginal teeth with highly eroded cusps.

We also recorded occasional animal remains, mostly chaetae of oligochaetes, some statoblasts of *Phumatella* sp. (Phylactolaemata), shells of newly hatched *Heleobia parchappii* (d'Orbigny) (Gastropoda: Hydrobiidae), fragmented rotifers, and microcrustacean appendages.

Figure 2 shows the relative abundance of the different food categories in the digestive tube of *Biomphalaria*, *Chilina*, and *Physa* (irrespective of the body size) as compared with the organic particles in the substrate samples from late spring. The composition of the crop contents in the three species showed a great similarity to the substrate composition. The only significant differences were due to a higher proportion of non-filamentous algae in the crops of *B. peregrina* and *P. venustula* ( $t = 3.68$ ,  $df = 23$ ,  $P$

$< 0.001$ , and  $t = 4.86$ ,  $df = 21$ ,  $P < 0.0001$ , respectively).

The results of PCA performed on the diets (sand excluded) are shown in Table 1 and Figure 3. The first component was highly positively correlated with the relative abundance of Di, and highly negatively correlated with NF. Snails whose diet included more Di relative to NF scored highly on this component. The second principal component was highly positively correlated with Di and highly negatively correlated with De. Stomachs with high content of Di relative to De scored highly on this component.

There was a high degree of diet overlap among the three species, but PCA still revealed interspecific variations. The mean principal component scores of the three groups differed significantly for PC1 and PC2 (one-way ANOVA test, Table 1). The multiple comparison (Scheffé test) revealed that *Biomphalaria peregrina* is more detritivorous, *Chilina parchappii* ingests more diatoms, and *Physa venustula* ingests more non-filamentous algae.

Some seasonal variations in the abundance of the different items could be detected (Figure 3). The isolated position of the autumn (April) samples of *Physa venustula* was mostly due to the high content of non-filamentous algae, represented in this case by *Euglena* spp., a kind of organism that never appeared in the other snail species or on other sampling dates.

In the laboratory experiments, *Physa venustula* showed the highest rates of ingestion and egestion ( $P < 0.05$ ), whereas *Biomphalaria peregrina* always had the second highest position (Figure 4). The values for *Chilina parchappii* were extremely low as an outcome of its peculiar behavior. *Physa* and *Biomphalaria* remained on the colonized artificial substrates most of the time during the feeding experiment, and browsed actively on the slides with the radula. *Chilina* instead crawled around and across the Petri dishes, with few buccal movements, even when they passed over the slides, leaving a large amount of mucus on the substrata.

Assimilation efficiencies ranged from 34% to 82%, with the lowest mean value achieved by *Physa venustula*.

## DISCUSSION

Many authors have shown that freshwater pulmonate snails are non-selective, microphagous animals. In this category are included, for example, several species in the genera *Lymnaea*, *Helisoma*, *Biomphalaria*, and *Bulinus* (Calow, 1970; Hunter, 1980; Baluku et al., 1987; Smith, 1989; Adam & Lewis, 1992; Madsen, 1992). The differences in the diet of snails living in different water bodies mainly reflect the variation in the composition of the *Aufwuchs*. Dillon & Davis (1991) even proposed using snail stomach contents as samples of the local diatom assemblages.

The close similarity between the organic particle com-

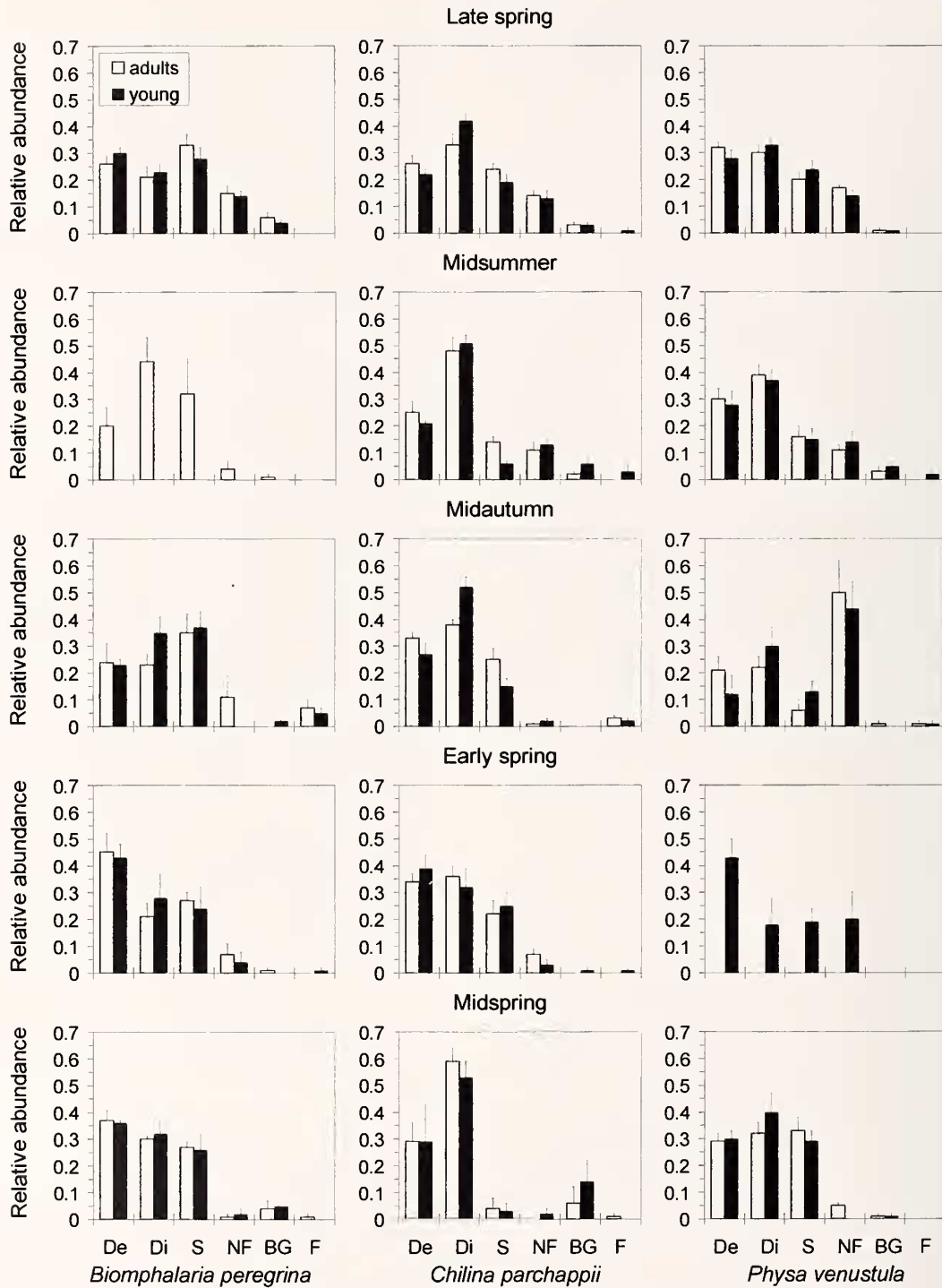


Figure 1. Crop content (mean + SE) of *Biomphalaria peregrina*, *Physa venustula*, and *Chilina parchappii* from an artificial canal in Buenos Aires province. De, detritus; Di, diatoms; S, sand; NF, non-filamentous algae; BG, blue-green algae; F, filamentous green algae.

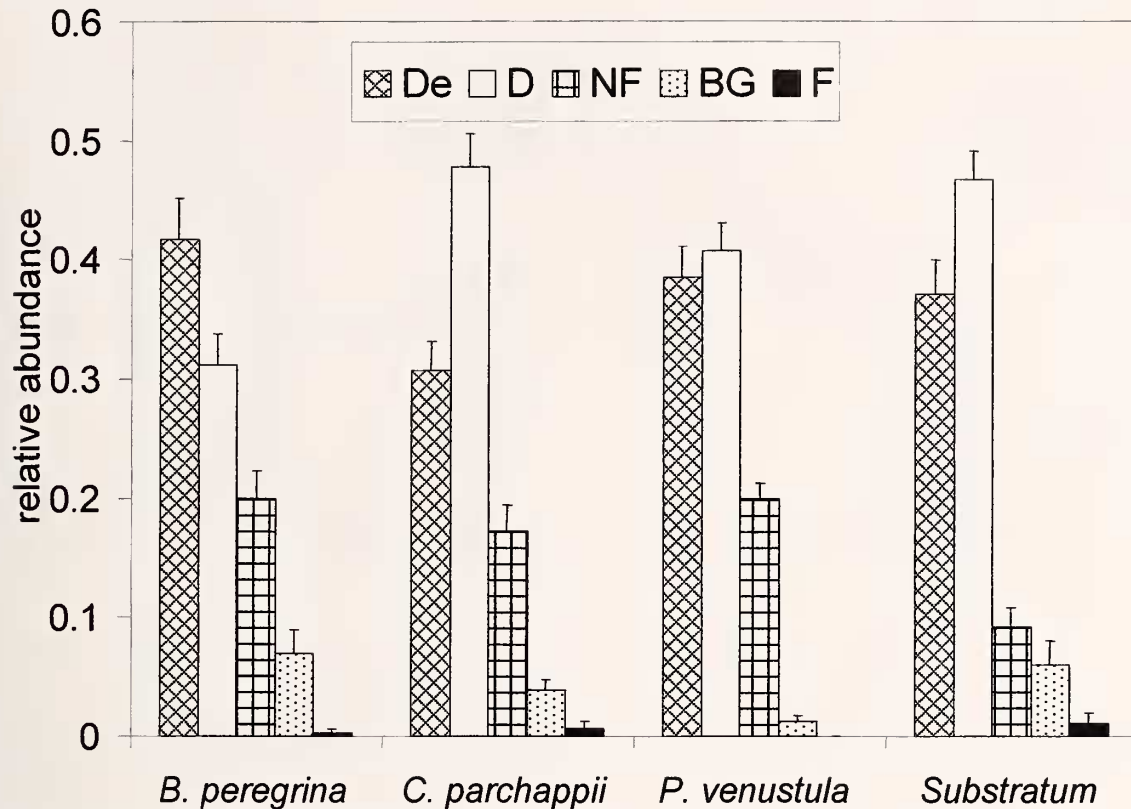


Figure 2. Crop content (mean + SE) of *Biomphalaria peregrina*, *Physa venustula*, and *Chilina parchappii* and the relative abundance of organic particles in the substrate samples from late spring. Abbreviations as in Figure 1.

position of the sediment and the crop contents of the three species studied suggests that they are basically non-selective feeders. When these animals feed on the same substrate, their diets are similar, and the diet composition does not differ from the *Aufwuchs* composition. The differences found among our snails are most probably due to the microdistribution of the patches of periphyton, resulting in a wide intraspecific variability.

Nevertheless, *Biomphalaria peregrina* exhibited a stronger tendency to eat more detritus than *Chilina* and *Physa*. This is consistent with the microdistributional information by Martín (1999) who stated that *B. peregrina* reaches its maximum abundance in the middle basin of the Napostá Grande stream, and that detritus affects its distribution. The middle basin receives organic contamination from a wide agricultural area, and effluent from the city. This portion of the stream was considered as mesosaprobic (Cazzaniga & Curino, 1987; Pettigrosso & Cazzaniga, 1987).

The lack of ontogenetic differences in the diet of the three species studied here is consistent with previous reports on *Biomphalaria pfeifferi*, *Helisoma duryi*, *Bulinus truncatus*, and *Bulinus forskalii* (Baluku et al., 1987; Madsen, 1992).

Many freshwater pulmonates carry sand particles in

their stomachs as a means of food grinding (Storey, 1970; Calow, 1973a; Reavell, 1980). Underwood & Thomas (1990) suggested that these mineral particles should also be a source of ions, micronutrients, and microorganisms. *Lymnaea peregra* shows low growth rates if its diet is devoid of mineral particles (Storey, 1970). *Biomphalaria glabrata* (Say) actively swallows sand and is able to select the size of the particles it retains in its digestive tube (Schmolder & Becker, 1990). Reavell (1980) found a very low proportion (and even absence) of sand grains in the diet of *Physa gyrina* (Say), indicating that the diameter of the mouth was a physical barrier to its ingestion. This does not seem to be the case in *P. vernalis* Taylor & Jokinen, where the sand grains can compose up to 15% of the diet (Kesler et al., 1986), or in *P. venustula* from the Napostá Grande stream (19%).

Blue-green and filamentous green algae are not important items in the diet of *Biomphalaria*, *Chilina*, and *Physa* in the studied area, as revealed by the low proportion of these items in their crops throughout the year. Other pulmonate species seem to prefer filamentous green algae (Lodge, 1986). Madsen (1992) determined that *Biomphalaria pfeifferi*, *Bulinus truncatus*, and *Lymnaea natalensis* are able to select against blue-green algae. The toxicity of some blue-green algae and their mucopolysac-

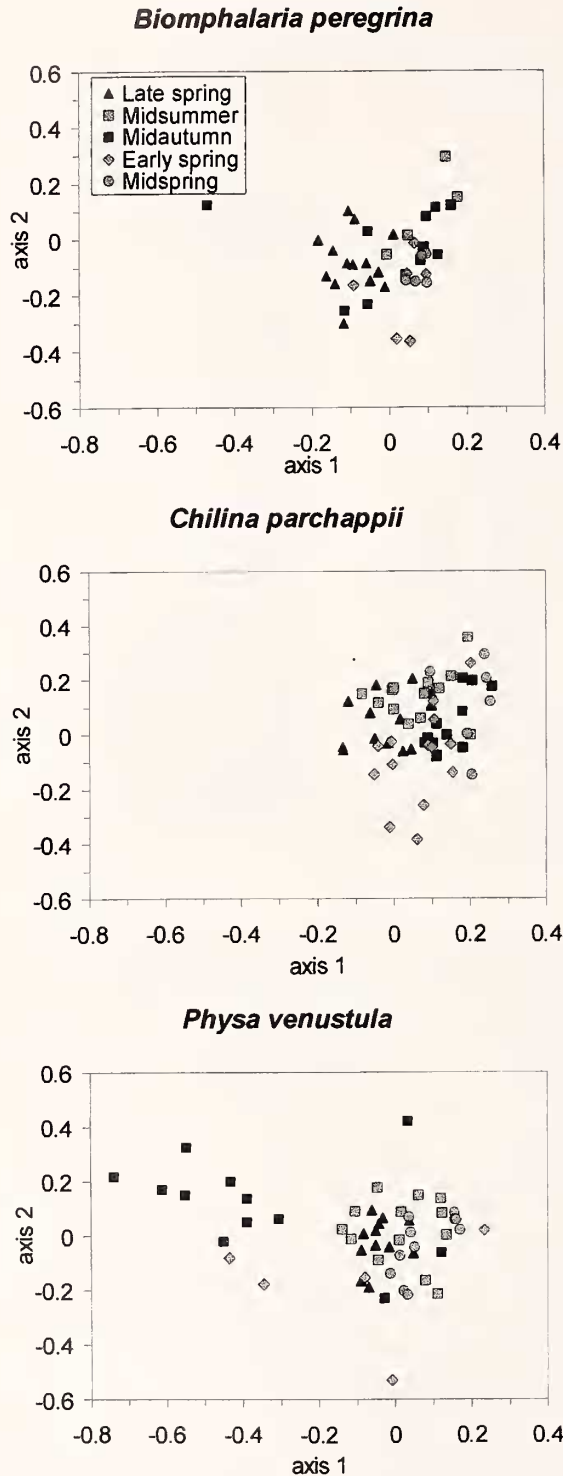


Figure 3. Crop content variations of *Biomphalaria peregrina*, *Physa venustula*, and *Chilina parchappii* based on the first and second principal component scores.

Table 1

Eigenvalues and component loadings for the first two principal components for *Chilina parchappii*, *Biomphalaria peregrina*, and *Physa venustula* based on crop contents.

	PC1 loadings	PC2 loadings
Diatoms (Di)	0.6332	0.7093
Non-filamentous algae (NF)	-0.9230	0.3015
Filamentous green algae (F)	0.0758	0.1232
Blue-green algae (BG)	0.0519	0.1865
Detritus (De)	0.3187	-0.8278
Eigenvalues	0.0297	0.0232
%variance explained	48.82	38.16
F-Value*	14.39	7.16
P	0.00001	0.0011

\* From ANOVA of the three species means of the principal component scores.

charide sheet should account for their low palatability. Some pulmonate species, however, have been successfully reared under laboratory conditions on a diet of blue-green algae (Skoog, 1978; Itagaki, 1987). It is probable that the low concentration of these algae in the stomachs of all of our snails was due simply to their low density in the substrate.

Diatoms eaten by *Biomphalaria*, *Chilina*, and *Physa* showed a variety of forms, sizes, and habits. Underwood & Thomas (1990) pointed out that certain anatomic traits or growing forms of algae can reduce the probability of being swallowed by different species of invertebrates. Hunter (1980) stated that *Cocconeis* is able to escape snail predation as an outcome of its morphology. Nevertheless, Smith (1989) and Dillon & Davis (1991) proposed that snails sample the diatom flora almost randomly, with only a few larger species under-represented in the gut contents. In this study we recorded a diversity of diatoms, from the small ovoid *Cocconeis*, to the elongated and narrow forms of *Synedra*, or the robust *Amphora*. There exists, however, a dominance of mobile diatoms (*Navicula*, *Nitzschia*, *Fragilaria*) and those living attached to the substrate by mucilaginous peduncles (*Cymbella*, *Rhoicosphenia*, *Gomphonema*). Due to their low level of adherence, these diatoms appear to be more vulnerable to attack by snails.

*Biomphalaria peregrina*, *Chilina parchappii*, and *Physa venustula* do not eat macrophytes. The scarcity of macrophyte fragments in their diet is consistent with other reports in the literature (Brönmark, 1990; Underwood & Thomas, 1990; Madsen, 1992). Leaf hardness seems to be one of the main reasons why pulmonates refuse to eat aquatic plants. The loss of a significant number of radular teeth has been correlated with the consumption of macrophyte material, and the use of macrophytes as food has